PERGAMON

Vision Research 41 (2001) 1915–1930

Vision Research

www.elsevier.com/locate/visres

Contextual influences on orientation discrimination: binding local and global cues

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Received 10 July 2000; received in revised form 21 February 2001

Abstract

We sought to determine how local and global features within an image interact by examining whether orientation discrimination thresholds could be modified by contextual information. In particular, we investigated how local orientation signals within an image are pooled together, and whether this pooling process is dependent on the global orientation content present in the image. We find that observers' orientation judgments depend on surround contextual information, with performance being optimal when the center and surround stimuli are clearly distinct. In cases where the center and surround were not clearly segregated, we report two sets of results. If there was an ambiguity regarding the perception of a global structure (i.e. a small mismatch between local cues), observers' performance was impaired. If there was no mismatch and local and global cues were consistent with the perception of a single surface, observers performed as well as in the distinct surfaces case. Although some of our results can be largely accounted for by interactions between differently oriented filters, other aspects are more difficult to reconcile with this explanation. We suggest that low level filtering constrains observers' performance, and that influences arising from image segmentation modify how local orientation signals are pooled together.

Keywords: Contextual influences; Orientation discrimination; Cues

1. Introduction

The processing of information in the early stages of the visual system is attributed to neurons which have been likened to linear filters, selectively processing components of a visual stimulus falling over their classical receptive field (i.e. Maffei & Fiorentini, 1973; Tolhurst & Movshon, 1975; Tolhurst & Thompson, 1981; DeValois, Yund, & Hepler, 1982; DeValois, Albrecht, & Thorell, 1982; Pollen & Ronner, 1982). However, the recent finding that in certain neurons a stimulus presented outside of the receptive field (referred to as the non-classical receptive field) can influence the neuron's response when presented in conjunction with a stimulus in the receptive field, suggests that some neurons are capable of signaling more complex or global features.

The discovery of the non-classical receptive field highlighted an important feature of visual processing; namely that the perception of a structure or a visual stimulus is strongly dependent on the context in which it is presented. This implies that fragments of images are not processed in isolation, but rather are interpreted as part of a whole, global structure. However, how this piecing together of the components of an image is achieved is a subject of debate. Two general ideas have been used to account for these effects. The first one suggests that interactions (long or short range) between oriented spatial frequency filters in the early stages of visual processing could lead to the contextual effects (e.g. Polat & Sagi, 1994a,b; Wolfson & Landy, 1999). In the second hypothesis, more complex processing based on both the local and global properties of the image are thought to influence perception by restructuring the properties of the receptive field (e.g. Caputo, 1996, 1997). In this hypothesis, the initial outputs of low level filters are insufficient to account for the results. Further processing, possibly in the form of feedback, is required to produce the contextual effects.

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PII: S0042-6989(01)00082-7

In order to examine how local signals in an image interact, psychophysical and physiological experiments have begun to examine the effects of adding flanking stimuli on the processing of a central stimulus.

1.1. Physiological results

Using single unit electrophysiology, most studies report the existence of suppressive/inhibitory interactions between the classical receptive field and non-classical receptive field when the stimuli within these two regions are roughly co-aligned (Nelson & Frost, 1978; Li & Li, 1994; Sillito, Grieve, Jones, Cudeiro, & Davis, 1995; Li, Thier, & Wehrhahn, 2000). However, more recently the existence of both inhibitory and excitatory effects have been found to depend on the relative contrast as well as the distance between the center and surround stimuli (Levitt & Lund, 1997; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998). The above studies all report that at suprathreshold contrast levels, the presence of collinear flanks act to suppress the neuron's response. One study, however, by Kapadia, Ito, Gilbert, and Westheimer (1995) reports excitatory influences using bar stimuli when these are co-aligned over the classical and non-classical receptive field.

These experiments employing stimuli falling outside of the classical receptive field yet eliciting a change in the neuron's response are similar in essence to those examining contextual modulation (Zipser, Lamme, & Schiller, 1996) or figure-ground segregation (Knierim & Van Essen, 1992; Olavarria, DeYoe, Knierim, Fox, & Van Essen, 1992). In these cases, the critical component is the existence of a clearly segregated boundary between two regions which most often led to an increase in a neuron's firing rate.

1.2. Psychophysical results

The majority of psychophysical experiments examining the effect of a surround on observers' performance have been carried out using contrast detection or discrimination paradigms which will be discussed below.

1.2.1. Apparent contrast tasks (supra-threshold tasks)

In experiments where subjects were required to judge the apparent contrast of a central stimulus embedded in a surround pattern, most researchers report a suppressive effect of the surround (Cannon & Fullenkamp, 1991; Snowden & Hammett, 1998; Solomon, Sperling, & Chubb, 1993). That is, the central stimulus was judged to be of a lower contrast than in the absence of the surround, and the amount of suppression was correlated with the degree of spatial similarity between the center and surround patterns. The maximum contextual effect occurred when the center and surround were of similar spatial frequencies and orientations.

1.2.2. Contrast detection tasks (threshold tasks)

In these experiments contrast detection thresholds are measured in the presence and absence of surround patterns. In general, the presence of collinear flanks at the same orientation and spatial frequency are found to have a facilitatory effect. That is, detection thresholds are lower in the presence of flanks. However this effect is dependent on both their spacing and relative contrasts (Polat & Sagi, 1993; Yu & Levi, 1998; Solomon & Morgan, 2000), as well as on the phase of the elements (Williams & Hess, 1998). Finally, Polat and Norcia (1996) and Polat and Tyler (1999) report that the optimal spatial configuration for the facilitatory effects of surrounding gabors on contrast detection of a central gabor occurs when these are arranged in an elongated manner along the length axis.

The above tasks have reported contextual effects using stimulus setups similar to those used in physiology (e.g. a central gabor patch surrounded by flankers). However, a different type of task which can be used to probe contextual effects involves using texture defined stimuli. In these tasks, observers are required to make detection or discrimination judgments on a line or a gabor, which is embedded within different spatial structures. These tasks are motivated by the idea of perceptual binding, or how local judgments can be affected by the degree of local-global coherency within the image.

1.2.3. Texture tasks

In these tasks a target is embedded in different patterns and observers are required to detect, and in certain cases discriminate, the target from the background. Wolfson and Landy (1999) and Caputo (1996, 1997) measured detection and discrimination thresholds for a line singleton embedded within a background texture of lines (separated by a small patch of intermediate lines). Both studies report that at short presentation times detection and discrimination thresholds for the target were increased when it was of the same orientation as the background. Caputo (1996, 1997) interprets these results as figure binding, whereby interactions between the target and surround occur if these can be perceptually bound together. In an experiment designed to assess the relative contribution of early filtering on a texture discrimination task, He and Nakayama (1994) report that observers' performance was dependent on higher order surface properties of occlusion and depth perception of the texture elements and could not be entirely accounted for by early cortical filtering. Both He and Nakayama and Caputo appeal to higher order image processing to account for their results.

Wehrhahn, Li, and Westheimer (1996) measured orientation discrimination thresholds of a target line which was masked by spatially overlapping patterns. They report that the presence of a masker impairs performance. However, the specificity of effects as well as their spatial distribution were not extensively examined. More recently, Li, Thier, and Wehrhahn (2000) examined orientation discrimination in humans and monkeys and found that orientation thresholds were raised in the presence of surrounding patterns. This effect was strongest for surround patterns which were parallel to the target line. The authors interpret their results as inhibitory influences arising in the form of feedback from higher level visual areas.

Contour binding tasks (Field, Hayes, & Hess, 1993; Kovacs & Julesz, 1993) have been designed to examine the rules underlying the association of elements as belonging to one object or not. It has been reported that observers' thresholds for detecting a contour (a spatial alignment of elements judged to be sufficiently similar in structure to be associated together) in noise is dependent on the relative orientation between the components of the contour, their spatial frequencies, phases and the separation between the elements.

1.2.4. Visual illusions of orientation

In these experiments the global perception of an object is systematically misjudged. This is most often attributed to adaptation after-effects (Gibson & Radner, 1937) or local interactions of orientation cues within the object. Examples of the latter are the Fraser and Zollner illusions (Oyama, 1973; Tyler & Nakayama, 1984; Morgan & Baldassi, 1997; Popple & Levi, 2000). In these illusions, subjects reportedly misjudge the overall orientation of a line composed of many locally oriented lines. The line itself is typically judged to be slanting away from its actual orientation because of the local orientation signals within it. Recently, Popple and Sagi (2000) have reported that this phenomenon is also dependent on the phase of the local elements comprising the line.

In the experiments described below we sought to examine systematically the effects of a surround pattern on observers' ability to discriminate orientation, in order to investigate how local and global cues interact. In the first set of experiments, we examined whether orientation discrimination thresholds could be influenced by surrounding patterns as had been reported by Wehrhahn et al. (1996) and Li et al. (2000). However, we sought to examine this systematically as a function of the similarity in the spatial structure between the center and the surround patterns. We found that presenting surround patterns of a similar orientation and spatial frequency markedly impairs observers' performance. When the surround and center patterns were dissimilar, the surround ceased to have an effect on observers' performance. Varying both the spatial and orientational differences between the center and surround also enabled us to measure the bandwidth of the surround's effects. These initial findings led to the issue of how the difference in the spatial structure of the center and surround might influence performance. In a second set of experiments, we wished to determine whether the key factor limiting observers' performance was the perceptual segregation of the center and surround, which might affect performance by drawing visual attention immediately to the target, or whether performance could be accounted for by simple interactions between oriented filters. In order to test these different explanations we examined the effect of adding local offsets (in phase or orientation) between the center and surround patterns in the cases where these were similar spatially. Finally, we sought to examine the spatial extent of surround influences on observers' performance by presenting portions of the surround pattern in different spatial locations. We find that there exists a spatial anisotropy of the contextual effects on orientation discrimination, with the maximal interactions occurring along the main axis of orientation.

2. Methods

2.1. Apparatus and stimuli

The stimuli were produced on-line using a Macintosh G3 and displayed in the center of a Sony Triniton monitor. The monitor was viewed binocularly at a distance of 114 cm, had a mean luminance of 36 cd m^2, and was calibrated using a UDT photometer. The screen resolution was 1024×768 pixels (60 pixels per degree of visual angle) and was refreshed at 85 Hz. Stimulus generation, presentation, and observers' responses were all computer controlled and stored online. Experiments were run from within Matlab, using both Psychtoolbox (Brainard, 1997) and Videotoolbox (Pelli, 1997) routines.

Orientation discrimination tasks were performed on a central stimulus which consisted of a circular patch of a 2 cpd sinusoidal grating measuring 3.1° in diameter. In the conditions employing a surround stimulus, the center and surround stimuli taken together covered 7.6 $degrees^2$. In the initial experiments the surround consisted of a sinewave grating. In a later series of experiments, bandpass filtered noise was used as a surround and will be described below. The central patch stimulus was always separated from the surround by a gap whose luminance was equal to the mean luminance of the display.

In each experiment, a two-alternative forced choice stimulus procedure was employed. Observers were presented sequentially with two stationary stimuli and were required to judge whether the orientation of the second stimulus was shifted clockwise or counterclockwise relative to the orientation of the first stimulus. The sequence was as follows: a fixation point was presented

(100 ms) followed by the first stimulus presentation (250 ms). A brief period (ranging from 500 to 750 ms) where the screen returned to mean luminance ensued prior to the presentation of the second stimulus (250 ms). The observers' task was to indicate by a keypress whether the stimulus shift between the two presentations had been clockwise or counterclockwise. Auditory negative feedback was provided on observers' errors. The phase of the central patch gratings was randomized between the two presentations so as to prevent observers from tracking the ends of the grating and from using information about location rather than orientation to perform the task. The orientation shifts that were tested varied between the different observers and were randomly chosen from a pre-determined set of test values.

Stimuli were presented at 30% contrast. Examples are illustrated in Fig. 1. Two initial conditions were tested: a '$\pm$ collinear' surround condition, whereby the central patch and surround were aligned (plus or minus a small orientation offset added to the surround only as will be described below; see Fig. 1a), and a 'perpendicular' surround condition, whereby the central patch was perpendicular to the surround (also, with an offset added to the surround; see Fig. 1b). In all conditions involving a surround, the surround stimulus was shifted between the two presentations by the same amount as the center.

2.1.1. Rationale for adding an orientation offset to the surround

The orientation offset was introduced initially to minimize any possible phase relationships between the center and surround gratings. The purpose of this was to force observers to use only the central patch to perform the task, preventing them from scanning the center and surround in an attempt to integrate the two (the issue of spatial integration will be the focus of Experiment 4 presented below). Although this is only a concern in the $\pm$collinear case, we added the same offset to the perpendicular case so as to maintain consistency across conditions. In all cases, the orientation offset was calculated to be half of the orientation shift being tested in the given condition, and then was set randomly to be positive or negative before being added to the surround. The sign of the offset added to the surround was maintained within each two-flash presentation, but varied after each two-flash presentation.

2.1.2. Rationale for randomizing the sign of the offset to the surround after each two flash presentation

This was done to avoid introducing orientation information at the gap which could be used to anticipate the shift. Within each two-flash presentation, the relative orientations of the center and surround were preserved since the surround was rotated by the same amount as the center between the two flashes. However after each two-flash presentation, the sign of the orientation offset added to the surround was re-set randomly to be either positive or negative. Hence, the relative orientations between the center and surround in the first flash could not be used to anticipate the sign of the orientation shift (see Fig. 2 for illustration).

2.1.3. Rationale for shifting the surround by the same amount as the center between the two flashes

In all conditions involving a surround stimulus, the surround was rotated by the same amount as the central patch in the second presentation. This was done to prevent observers from comparing the location of the edges of the central grating with those of the

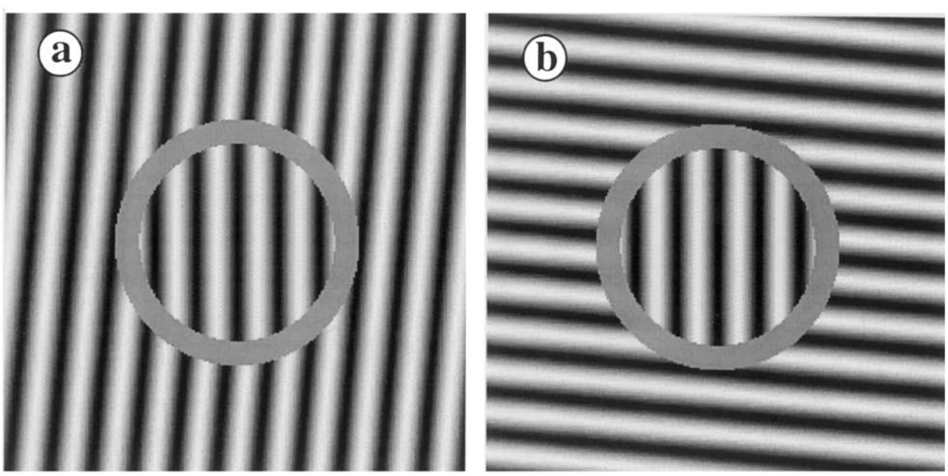

Fig. 1. Examples of the basic stimuli used in experiment 1. (a) $\pm$collinear condition consisting of a central patch of a 2 cpd sinewave grating embedded in a surround of a similar spatial frequency and orientation; (b) perpendicular condition where the surround grating is approximately orthogonal to the orientation of the central patch.

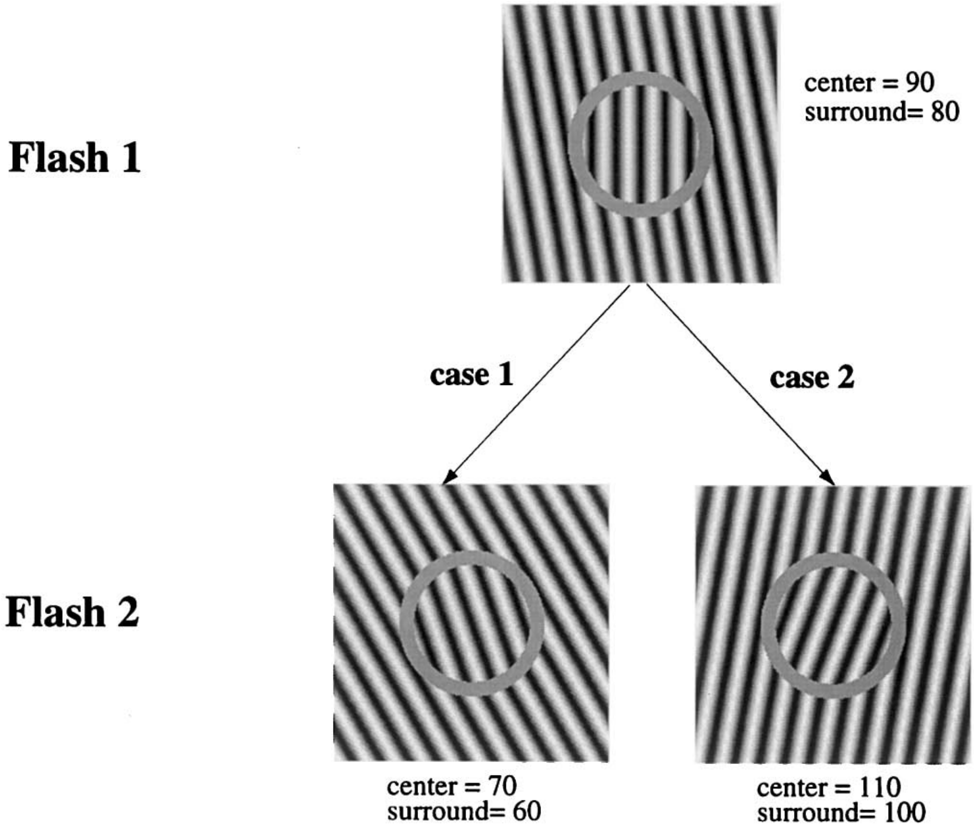

Fig. 2. Example of effect of randomization. In this illustration, the shift tested will be 20°.The offset added to the surround could be either −10 or +10° (in this illustration, it is shown as −10°). Although there is a clear orientation cue between the center and surround in Flash 1, it can not be used to anticipate the direction of the shift because either of case 1 or case 2 are likely to occur.

surround between the two presentations. Although it is conceivable to perform the task solely on the surround, all observers were instructed to fixate the central patch. In addition, two observers attempted to perform the task using the surround and reported that the task was made more difficult under these conditions. The main difficulty was that, given the spatial layout of the stimulus, the surround was in peripheral vision and it was difficult to entirely ignore the center. Observers reported that they were aware of the center and were not confident that they were performing the task solely on the surround information. A possibility would be to make the center be mean gray luminance and only have a surround grating. However, this no longer approximates the task carried out, and would not address the issue of using the surround information when both center and surround are present.

2.2. Orientation discrimination thresholds

Thresholds were determined using a method of constant stimuli. The orientation of the stimulus in the first presentation was chosen randomly from a set of orientations centered around vertical and ranging from −45 to +45°. Sixteen levels of orientation shifts (eight positive and eight negative) were used to sample the psychometric function on the second presentation of the stimulus. Depending on the task and the observer, the smallest orientation step was 0.625° (shifts ranging from −5 to +5°), and the largest orientation step was 1.25° (shifts from −10 to +10°).

Observers initially familiarized themselves with the task prior to threshold collection. Typically observers performed the orientation tasks between 40 (center alone condition) and 80 times before data were collected to measure thresholds. One run consisted of 20 tests of the 16 orientation shifts and typically lasted 20 min ($16 \times 20 = 320$ presentations per run). Each level of orientation shift was sampled at least 200 times, except for observer SS who was no longer available for testing and was only sampled 100 times per data point. Two authors were experienced psychophysical observers, whereas the other observers were naive to the purpose of the study and underwent longer training periods prior to threshold measurements. All observers had normal or corrected to normal vision.

Observers' data on a given condition were pooled across the runs, and a bootstrapping procedure was used to fit a cumulative Gaussian (Foster & Bischof, 1991). The 75% correct point was chosen as the measure of orientation discrimination thresholds. Error bars on the plots represent the standard deviations of the thresholds at the 75% criterion levels and were derived from the bootstrapping procedure. Orientation biases inherent to individual observers were removed from estimates of thresholds. This was achieved by obtaining and removing the orientation shift at which the observer performed at 50% (this value should be 0 if no biases are present) from the orientation value corresponding to 75% correct. Bias estimates as obtained from the 50% threshold measure were small for all observers tested (between 0.1 and 0.5°).

3. Results

3.1. Experiment 1: orientation thresholds as a function of the orientation of a surround stimulus

Prior to measuring the extent of the surround pattern's influence on observers' performance in these experiments, we wished to optimize the spatial arrangement of the stimulus. Wehrhahn et al. (1996) and Li et al. (2000) found that the spatial separation between their target and masks (i.e. surrounds) played an important role in determining the magnitude of their effects. In a preliminary experiment, thresholds were collected for one observer as a function of the gap width separating the center and surround patterns for the $\pm$ collinear and perpendicular surround patterns.

Fig. 3 shows orientation thresholds for IM measured using a perpendicular surround (filled symbols) and a $\pm$ collinear surround (open symbols) as a function of the gap width separating the two patterns. The 'single' condition along the abscissa corresponds to the threshold measured when the center was presented

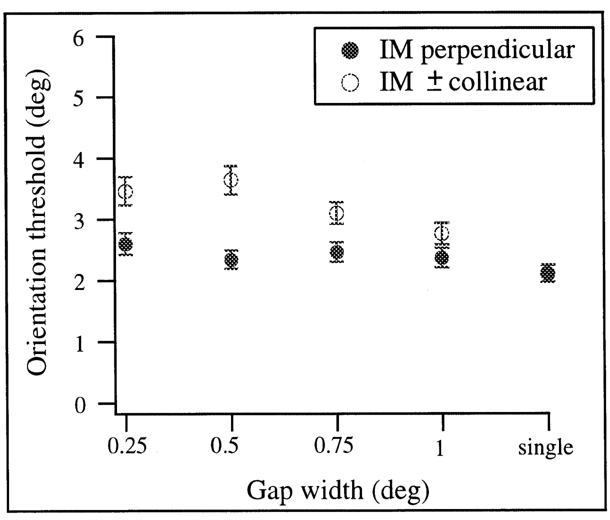

Fig. 3. Effect of gap width on orientation thresholds with $\pm$ collinear and perpendicular surrounds.

alone. Comparison of these two surround conditions highlights two important points. First, the presence of the $\pm$ collinear surround impairs performance (nearly two-fold at the 0.5° case), and second, the presence of a perpendicular surround does not significantly affect performance (compare single patch condition versus any of the perpendicular surround conditions). Only at the smallest gap width tested did the presence of the perpendicular surround slightly impair performance, most likely due to the increased confusability of the stimulus possibly due to crowding. In the $\pm$ collinear case, it is apparent that as the gap width is reduced, the detrimental effect of the surround on orientation thresholds increases, then seemingly plateaus at roughly a 0.5° separation. At the smallest width tested, it became increasingly difficult to dissociate the center from the surround. In all experiments presented below, a separation width of 0.5° was used. The gap width did not affect performance with the perpendicular surrounds for this observer.

Having found that orientation thresholds were affected by the surround pattern only for the $\pm$ collinear condition, we measured this effect in different observers at a gap width of 0.5°. The results are shown in Fig. 4, where orientation thresholds were measured in the absence of a surround (single condition) and with two different types of surrounds. Two points emerge from these graphs. Firstly, thresholds measured with a perpendicular surround are similar to those measured without a surround. This suggests that the presence of a perpendicular surround did not elicit any facilitation. Secondly, for all observers, the presence of a $\pm$ collinear surround raised the thresholds roughly 1.5-fold. The finding that a perpendicular surround has no effect on performance for this task suggests that it is being ignored. This could be due to the center and surround being clearly segregated such that attention is directed immediately to the center leading to the good performance. In this sense, this condition can be likened to the center alone condition, where a full field of mean luminance surrounding the central patch could be interpreted as a background from which the center is clearly segregated. Alternatively, the lack of effect of a perpendicular surround could arise from the processing of these two surfaces by independent neuronal pools, with no, or minimal interaction. In order to examine the effects of the spatial relationship between the center and surround in more detail, we initially estimated the orientational and spatial bandwidth of the surround's effects on performance.

3.2. Experiment 2: spatial and orientational bandwidths of effect

Fig. 5 plots thresholds measured as a function of the spatial frequency difference between the center and

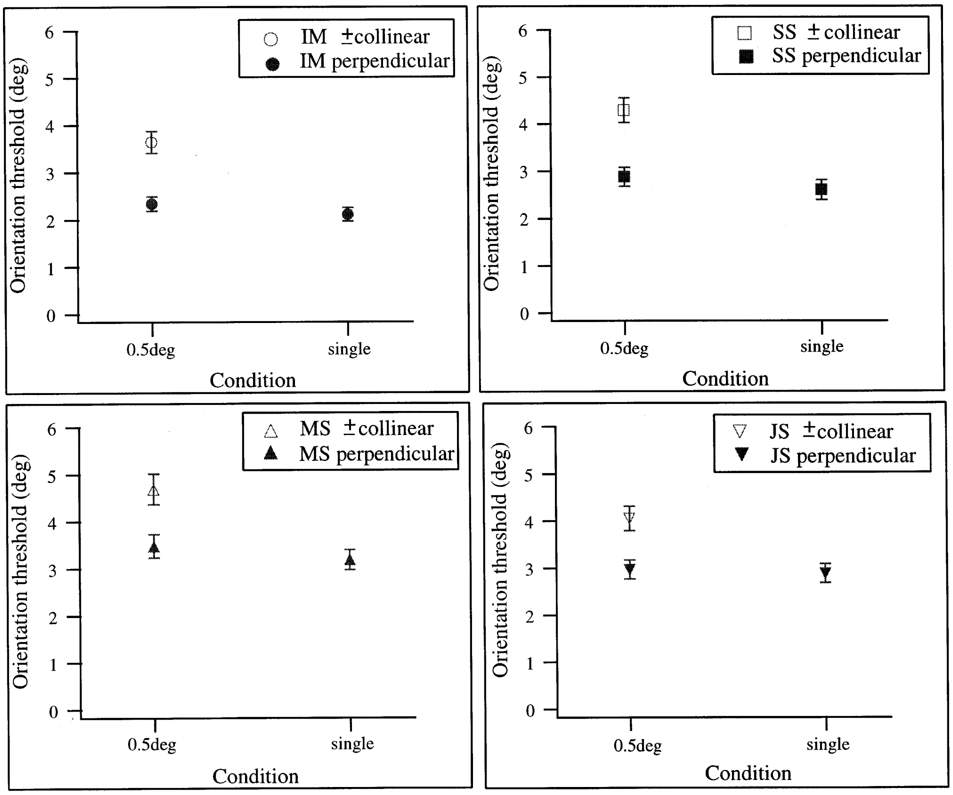

Fig. 4. Orientation discrimination thresholds for four subjects as a function of the surround orientation. Open symbols are with a collinear surround, filled symbols with a perpendicular surround. The single condition refers to orientation thresholds measured on the central patch without a surround.

surround (Fig. 5a, c) in the $\pm$ collinear condition. In this experiment, the contrast of the surround gratings was manipulated so as to be matched in apparent contrast with that of the center by a contrast matching procedure. This was achieved by presenting the stimuli for 250 ms, and increasing the contrast of the surround by steps of 5% until the observer perceived the center and surround as being of similar contrasts. The surround contrast at which the center and surround appeared matched was then used for the spatial frequency being tested. The dashed line corresponds to the observer's threshold measured with the single patch, and solid curves represent the best fitting Gaussian to the data. It is clear that surround patterns which differ in spatial frequency by 1.5 octaves still affect observers' performance, although much less than when the center and surround were of the same spatial frequencies.

When the orientation difference between the center and surround is manipulated, the same pattern of results arises (Fig. 5b, d). Bandwidths derived from the Gaussian fits are 35.2° for subject IM (half width at half height) and 43° for JS. As the difference between the center and surround gratings exceeds 45°, the effect of the surround decreases. However, thresholds never drop below the level measured without a surround, indicating the lack of facilitatory effect of the surround patterns on orientation thresholds.

These results reveal that the tuning of the surround effect is relatively narrow. This suggests an interactive relationship between the center and surround when these two are of relatively similar spatial structure. However, whether the inhibitory effect of the surround on orientation thresholds results from the pooling of two different orientation estimates (one for the center and one for the surround) which occurs when two surfaces are sufficiently similar, or from a higher level saliency signal which degrades performance when there is no strong segmentation cue between the center and surround, remains unclear. In order to differentiate between these possibilities we sought to devise a background that would be easily segmented, yet would lead to the same amount of low level filter stimulation. If in this case the presence of the surround still degrades performance, the most likely interpretation would be one of interactions between independent pools of neurons.

3.3. Experiment 3: effect of saliency of background segregation on performance

The aim of this experiment was to design a background that would easily segment, yet provide the same level of stimulation to low level filters as the grating background conditions. To achieve this we used noise backgrounds that were either filtered in their spatial frequency content (Section 3.3.1) or in their orientational content (Section 3.3.2).

3.3.1. Isotropic noise background

In the first part of this experiment, isotropic noise backgrounds were used. The noise patterns were generated from white noise textures and were filtered in the Fourier domain using bandpass spatial frequency filters with a bandwidth of 0.5 octaves, centered about the spatial frequency of the central patch grating (2 cpd). After filtering, the noise images were normalized to a root mean square (RMS) contrast of 30% and stored on line.

An example of this stimulus is illustrated in Fig. 6a. Observers were required to perform the same task as before, but now with the central patch being surrounded by an isotropic noise background. All baseline parameters (presentation duration, interstimulus time interval and gap width) were held constant.

The results of this experiment are plotted out in Fig. 7 for two observers. For comparison purposes, the thresholds measured from Experiment 1 have been included in the graphs. It is apparent that the use of unoriented noise as a background ('isotropic' condition) does not impair either observer's ability to perform the task. For both observers, the orientation thresholds are the same as measured using a perpendicular grating surround.

Had the presence of an isotropic noise background impaired observers' performance, this would have been strong support for interactions between oriented filters constraining performance levels. However, we find that the isotropic noise background does not affect performance. Unfortunately this negative result can be interpreted in either of two ways. A low-level filter explanation would postulate that in this experiment there is less energy in the narrow range of oriented filters which interact with those processing the center. Alternatively, the segmentation hypothesis would account for the result in Fig. 7 by proposing that since the central patch is clearly segregated from the surround, this leads to improved performance. However, present-

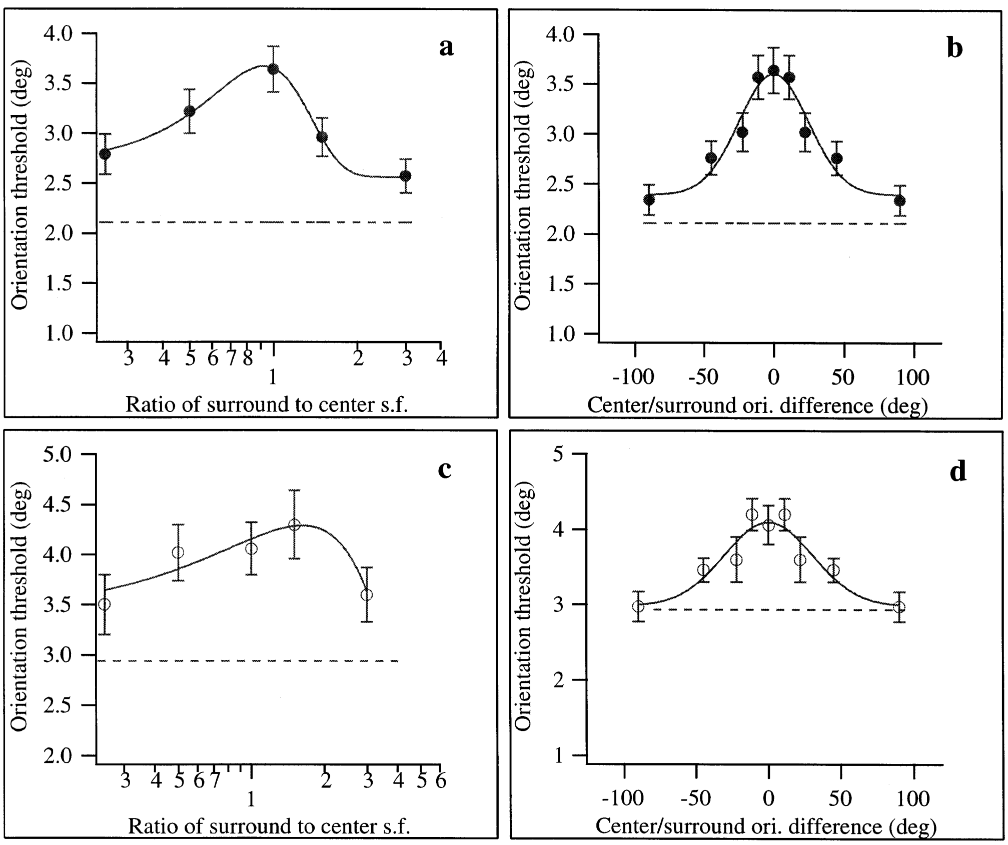

Fig. 5. Orientation and spatial frequency tuning of the effect. Orientation thresholds measured as a function of the difference in spatial frequency between the center and surround (in ± collinear case) in a and c, and as a function of orientation (same spatial frequencies) in b and d for two subjects. Filled symbols for subject IM, open symbols subject JS. Solid curve through the data points is the best fitting Gaussian, and dashed lines represent thresholds measured with the single patch alone.

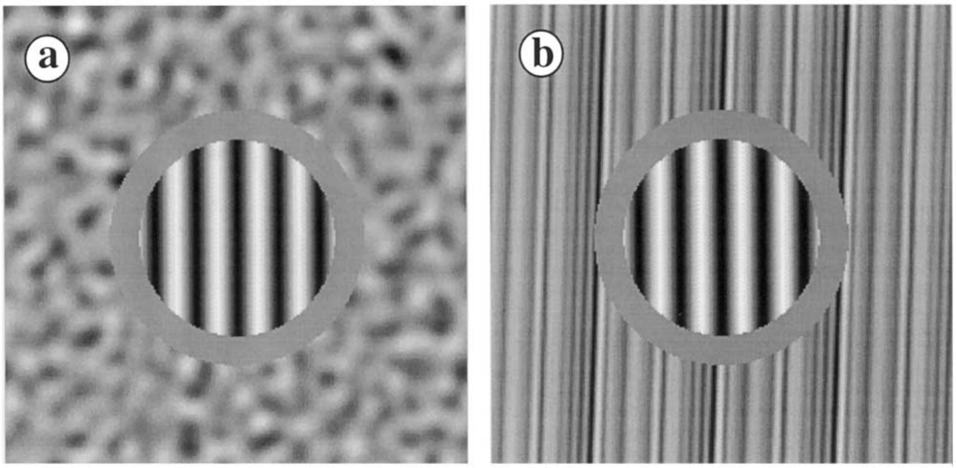

Fig. 6. Examples of stimuli used with noise backgrounds. (a) isotropic noise background; (b) oriented noise background consisting of the sum of six sinusoids straddling the central frequency by steps of 0.5 octaves.

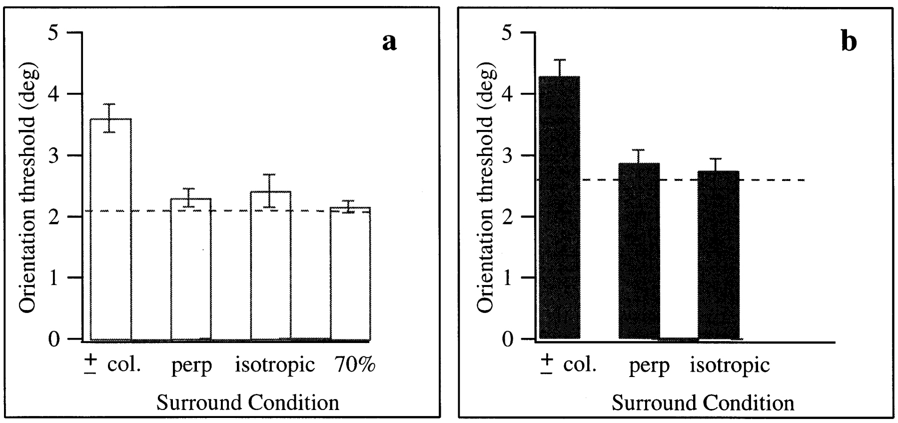

Fig. 7. Effect of different backgrounds on orientation thresholds. (a) subject IM thresholds measured using (from left to right), a ± collinear background, a perpendicular background, an isotropic noise background and an isotropic noise background at 70% contrast. Dashed line is the single patch condition; (b) same conditions for subject SS.

ing noise stimuli at 30% RMS contrast does not evoke a response equivalent in strength to that evoked by a 30% contrast sinewave that is optimal for a given orientation channel. One observer (IM) tested this stimulus with the isotropic noise at 70% RMS contrast and obtained similar thresholds to the 30% case (Fig. 7a, 70% condition). This supports the hypothesis that the effect is dominated by image segmentation cues rather than filter interactions. Indeed filter interactions would predict that at 70% contrast, thresholds should be raised as much as with a 30% contrast grating.

In a further attempt to determine which of the filter hypothesis or segmentation hypothesis could better account for our results, we used a different type of noise background. This noise stimulus was bandlimited in spatial frequency and orientation to stimulate collinear filters optimally, while it was also clearly segregated from the central patch. This stimulus will be described in Section 3.3.2.

3.3.2. Sum-of-sinusoids background

The background used in the following experiment consisted of the sum of six sinusoids of the same orientation but different frequencies (straddling the central patch frequency by steps of 0.5 octaves). This stimulus was used for two reasons; to limit the orientation bandwidth to only one orientation value, and to maximize the contrast energy along a narrow spatial frequency range about the central patch frequency. The phases of the sinusoids being combined in this stimulus were randomized in each presentation and images were normalized to 30% contrast. The sequence of the task was the same as in the above conditions. An example of the stimulus used is illustrated in Fig. 6b.

Results from four observers are presented in Fig. 8. All observers have significantly lower thresholds with the perpendicular noise background than with the ± collinear noise background. One observer (Fig. 8d), however, shows an improvement in performance with

± collinear noise compared to performance with ± collinear sinewave gratings in the surround. Note that for this observer, orientation thresholds decrease using ± collinear noise to a level approaching her performance using a perpendicular sinewave background. It appears that for this observer, segmentation cues were reliably used to improve performance. The other observers did not display this trend.

3.4. Experiment 4: role of gap and possible binding between two surfaces: effect of 'good continuity' or coherency across the gap

Finally, we sought to examine whether information at the gap suggestive of two separate surfaces (center and surround) would be sufficient to alter performance. This was achieved by measuring thresholds when the center and surround had no orientation offset between them and were either in phase, or out-of-phase by 180°. In the out-of-phase case, the center and surround are not clearly segregated perceptually (indicating one surface), yet there is a lack of continuity across the gap between the two (indicating two surfaces; see insets of Fig. 9 for illustrations).

Results of this experiment are plotted out in Fig. 9, and show that having only a phase offset between the center and surround is sufficient to impair performance. The thresholds were approximately the same as in Experiment 1 with the ± collinear background (compare ± col to phase condition in Fig. 9). Interestingly, when there was no offset in either phase or orientation (aligned condition), performance was much improved although, for both observers, thresholds did not reach the level of the single patch condition.

The difference in performance between the 'aligned' and out-of-phase conditions suggests that noise is being introduced during the pooling of the orientation signals when there is a phase mismatch between the center and surround. Simple-cell like filters overlapping the gap would most likely be insufficient to introduce the amount of noise required for the out-of-phase condition results. However they may be used to signal a discontinuity between the center and surround. This discontinuity signal could be made available to a higher level mechanism that might introduce additional noise during the combination of the two orientation signals.

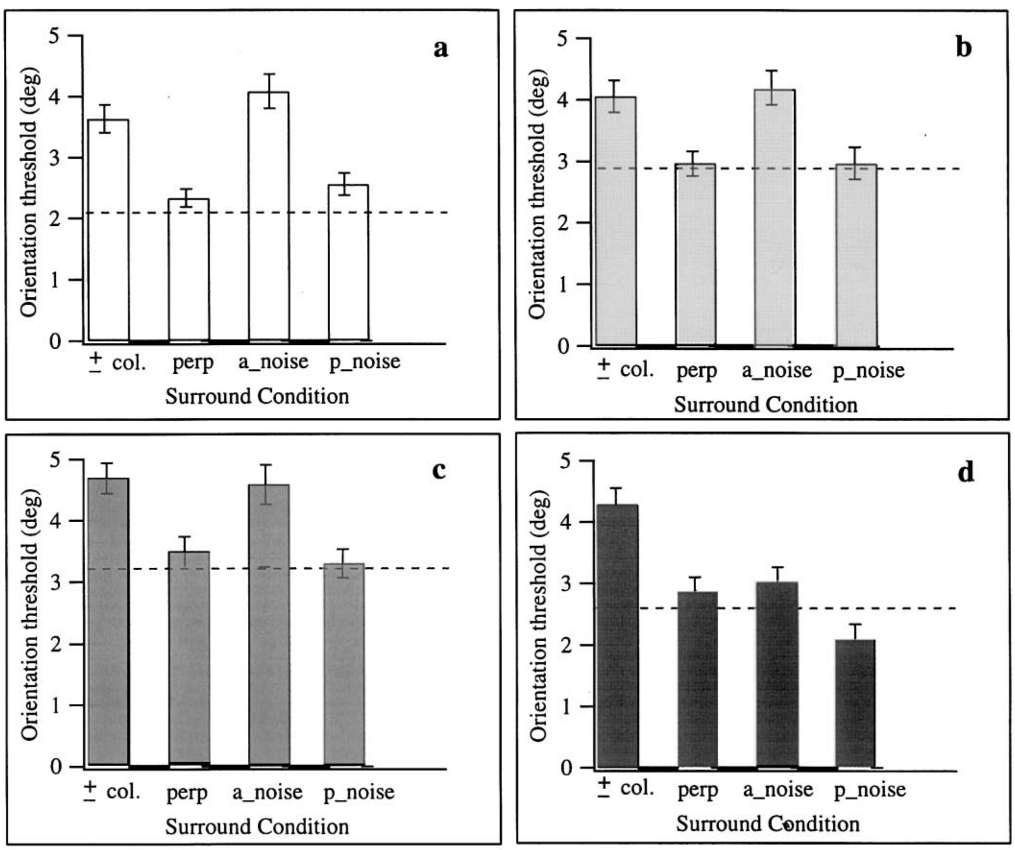

Fig. 8. Effect of different noise backgrounds on orientation thresholds. (a). subject IM thresholds measured using (from left to right) a ± collinear background, a perpendicular background, an aligned noise background(a_noise) and a perpendicular noise background (p_noise). Dashed line is single patch condition. See text for details; (b) same conditions for subject JS; (c) subject MPS; and (d) subject SS.

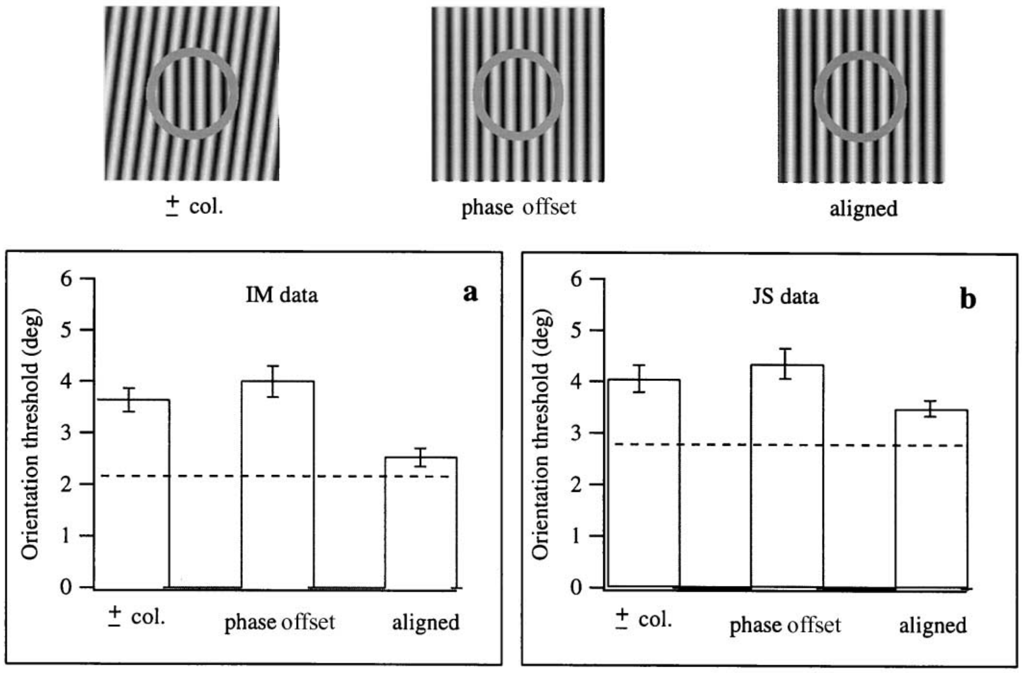

Fig. 9. Role of coherency (good continuity) between the center and surround in determining performance. (a) dashed line represents threshold for a single patch, for subject IM. The three conditions tested are illustrated above; (b) same conditions tested on subject JS.

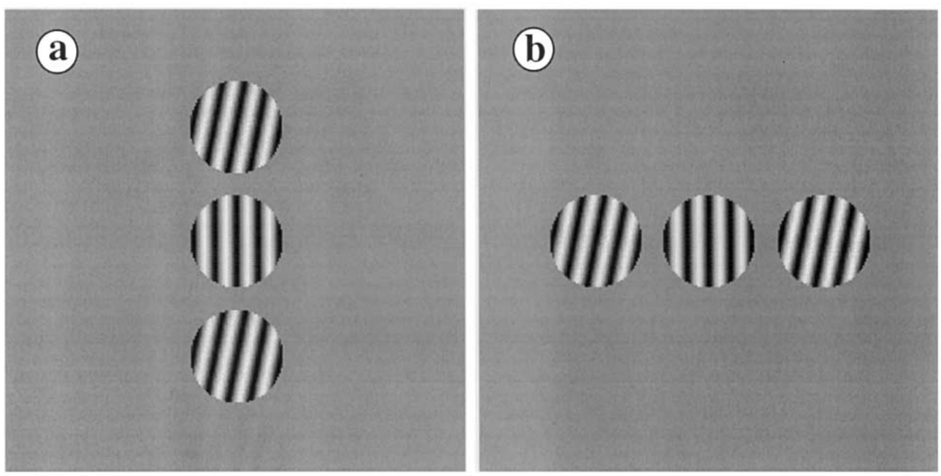

Fig. 10. Examples of the stimuli used in experiment 5. (a) flanks parallel condition with flanks parallel to the main axis of orientation; (b) flanks perpendicular condition with flanks perpendicular to the main axis of orientation.

3.5. Experiment 5: spatial extent of the effects

Finally, we assessed the spatial extent of the interactive effects between the center and surround by using a three patch stimulus, with the patches separated by 0.5° from one another. The stimuli were viewed at half the regular distance and were scaled in order to preserve both the size of the patch and the spatial frequency of the carrier. Two types of stimuli were used, one with the patches presented along the main axis of orientation (Fig. 10a, referred to as 'flanks parallel') and one with the three patches presented perpendicular to the main axis of orientation (Fig. 10b, referred to as 'flanks perp'). The procedure was the same in this experiment as in the previous ones with an orientation offset added on the flanking gratings. The only difference here was that the flanking patches were held stationary (i.e. kept in the same positions between the two flashes), to avoid introducing any localization cues on the flanking patches positions.

Results from this experiment are plotted out for two subjects in Fig. 11. The main finding in this experiment is that when the flanks are located along the perpendicular axis (Fig. 10b), thresholds are roughly the same as when the entire surround is present (compare 'flanks perp' condition, with the $\pm$col condition). However, when the flanks are presented along the main axis of orientation, thresholds are raised even more than in the regular full field surround ('flanks parallel' condition, compared to $\pm$ col). These results suggest that the main area of interaction is located along the ends of the stimulus as defined by the axis of orientation. In addition, this suggests that the strength of the effects along this axis are slightly reduced when flanking stimuli presented along the perpendicular axis are presented simultaneously. This is similar, in essence, to Solomon and Morgan (2000) who report that the facilitatory effects of collinear stimuli in a contrast detection task are canceled by the presence of non-collinear flanks. They suggest a non-linear mechanism which combines information anisotropically to account for their results.

These findings are also largely consistent with those of Polat and Sagi (1993), Polat and Norcia (1996) and Polat and Tyler (1999), who report interactions between flanks and a central gabor which occur mainly along the collinear axis (i.e. along the main axis of orientation). Similarly, Toet and Levi (1992) using a crowding procedure report that the major effects beyond the central 2° are anisotropic, occurring mainly along the collinear axis.

4. Controls

4.1. Adaptation, neural fatigue and tilt after-effects

A possible explanation for our initial results ($\pm$ collinear versus the perpendicular case) is that in the $\pm$ collinear either adaptation leading to a tilt induced effect, or neural fatigue might underlie the increased thresholds. Indeed, in the $\pm$ collinear cases there was always an orientation offset between the center and surround which could have induced orientation aftereffects. However, a number of our results rule this out. First of all, the adaptation hypothesis would predict that the out-of-phase and aligned conditions (Experiment 4, Fig. 9) should yield similar results, mainly that thresholds should approximate the single patch condition. This was not observed. We found that thresholds measured when the center and surround were out-of-phase were higher than those in the aligned conditions, despite the absence of an orientation offset between the center and surround patterns. In addition, the size of the tilt illusion is dependent on the orientation offset between two patterns, peaking when the two patterns are offset in orientation between 10–15°. Looking back at Fig. 5, we find that there is no significant difference in the orientation thresholds between 0 and 12.5° difference in the center and surround orientations. A tilt induced effect would have resulted in the 0° case having a smaller orientation threshold than the 15° case. Finally, we examined whether there was any bias in the errors made by the observers. Indeed, adaptation would suggest that fewer errors would be made when the orientation offset between the center and the surround are of the same sign as the orientation shift between the two flashes (i.e. are in the same direction). For example, discriminating a positive shift in orientation between the two flashes might be easier when there is a positive orientation offset between the center and surround gratings. To this end, we compared the errors made in the basic collinear surround case when the orientation shift was positive and the orientation offset was also positive (or both negative, respectively) to those made when one was positive and the other negative. For the two observers tested, there were no significant differences in the errors made in the different conditions.

The finding in Experiment 4 that there is a difference in performance for both observers between the aligned and out-of-phase conditions also controls against neural fatigue as an explanation for the differences in the $\pm$ collinear and perpendicular conditions. However, we also measured in one subject (IM) thresholds for a full

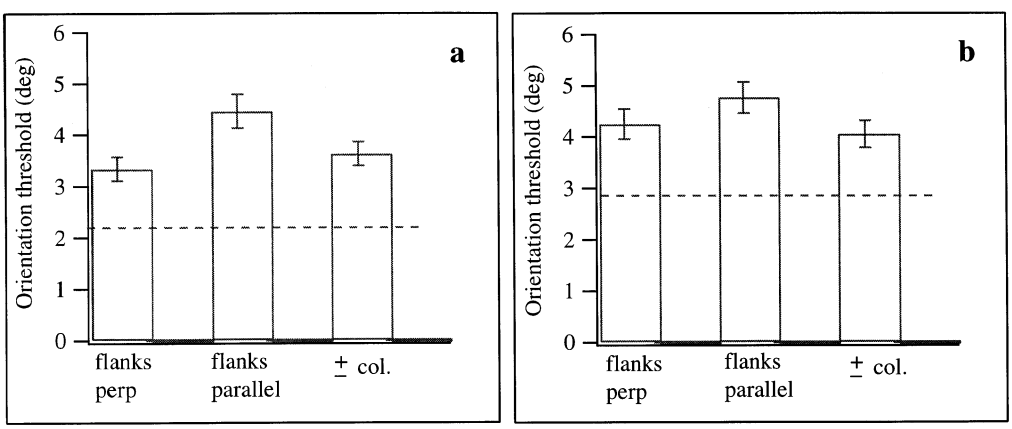

Fig. 11. Spatial localization of effects (a) subject IM , Flanks perp is the 3 patch stimulus with flanks perpendicular to the main axis of orientation. Flanks parallel is with the flanks along the ends of the main axis of orientation in experiment 1. Dashed line is the single patch condition; (b) same conditions tested with subject JS.

field stimulus. The threshold measured was $2.25 \pm 0.4°$, not significantly different from that measured to the single patch ($2.11 \pm 0.14°$). Since the diameter of the central patch exceeds the length at which orientation thresholds might vary (1°; Heeley & Buchanan-Smith, 1998), the full field and the single patch thresholds should be similar if the effect of neural fatigue is negligible.

4.2. Apparent motion

Although the stimuli were phase randomized between the two flashes and there was a relatively long ISI (between 500 and 750 ms), it is conceivable that observers perceive apparent motion between the two presentations which might influence their performance. Although this is a possibility, this would predict that observers would be better in the same orientation case because all motion cues would be in the same direction. However, in the perpendicular case there would be two strong orthogonal motion signals, one of the center target and one of the surround. If anything, these conflicting motion cues should impede performance, yet observers were as good in this condition as in the single patch condition. In addition, this hypothesis would predict similar performance for the aligned and out-of-phase conditions, which was not observed.

4.3. Oblique effect

The oblique effect is a well documented phenomenon, whereby observers are more sensitive to variations in orientation around vertical than around oblique orientations (e.g. Campbell & Kulikowski, 1966; Heeley, Buchanan-Smith, Cromwell, & Wright, 1997). In order to investigate whether the strength of the contextual influences we report shows a similar dependence on the absolute orientations tested, we separated our results into thresholds measured about the vertical ($\pm 5°$) and those measured about the obliques. This is illustrated in Fig. 12, for four observers. Open bars are thresholds measured at orientations about vertical, filled bars are thresholds obtained from the off-vertical ('oblique' conditions) orientation levels tested. Note that for observer MS, performance was too good with the perpendicular surround to measure a threshold in the vertical case. In the case of oblique orientations, all four observers displayed the similar trend of effects, namely that thresholds were raised in the presence of a $\pm$ collinear surround. In the case of the vertical orientations, only one observer (MS) showed a similar trend of results, with thresholds being raised in the presence of $\pm$ collinear surround. The other observers did not display much variation in thresholds across the different conditions. These results reveal that the effect of the surround on orientation thresholds is stronger for oblique orientations, suggesting that tasks specifically aimed at investigating orientation binding should not be limited to vertical orientations. In addition, this validates our use of a two flash presentation paradigm, because standard one flash orientation experiments requiring subjects to make judgments about vertical or horizontal would miss some of the effects reported here.

5. Discussion

To summarize the results presented in this paper, we find that orientation discrimination thresholds increase when a central target is embedded in a surround of a similar spatial structure. This effect is dependent on the respective spatial frequency and orientation of the center and surround.

We reach three conclusions regarding the pooling of orientation signals in an image:

1. If the center and surround are composed of different spatial structures, there is no interference of the background on the center target as indicated by orientation thresholds being similar to those measured with a single patch (see orthogonal background and isotropic noise results).
2. If the center and surround share some spatial characteristics, there can be interference, leading to raised thresholds (see oriented noise results).
3. If the center and surround are similar and
   - If information at the gap is inconsistent with one object, there is interference and thresholds are raised (see out-of-phase and orientation offset results).
   - If information at the gap is consistent with one object, there is no interaction and thresholds remain largely unaffected (see fully aligned case).

A portion of the results reported here could be accounted for by interactions between oriented filters which would constrain observers' performance. Since the bandwidth of the surround's effects on the center is relatively narrowband, it is possible to invoke neuronal pools that process the center and surround and that only interact when there is sufficient spatial similarity between these two structures. However, although the bulk of our results suggest that low level filtering could account for part of our data, cues arising from image segmentation cannot always be ignored. This is the case for the isotropic noise experiments, and also the oriented noise for which observer SS's thresholds were unaffected by a collinear noise background. These results are difficult to reconcile with simple filtering alone, and imply that, for different observers, segmentation cues influence performance differentially.

Fig. 13 illustrates conceptually how simple-cell like filters tiling the spatial extent of the stimulus could be excited in the conditions that we examined. For the moment, we specifically leave out influences from

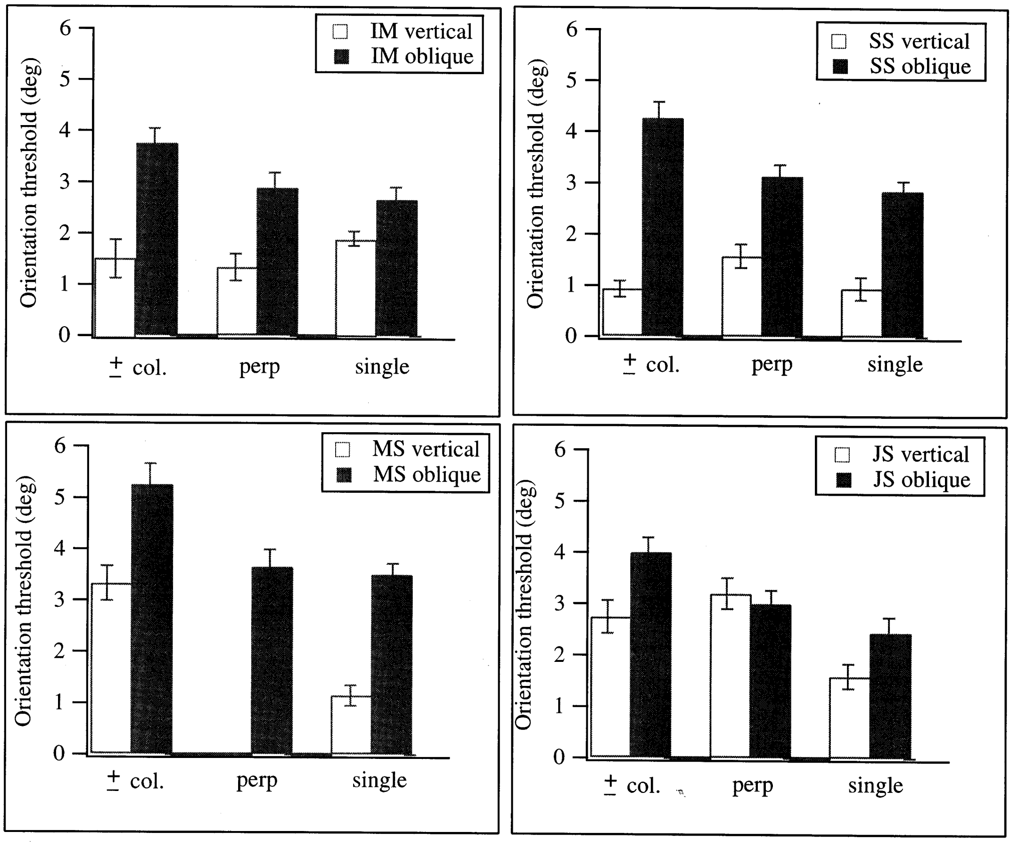

Fig. 12. Oblique effect results. Open bars are thresholds measured around vertical (flanking 5° on either side), filled symbols are for oblique orientations.

segmentation. In (a) (orientation offset) and (c) (phase offset), a filter covering the gap could signal a discontinuity by reducing its input into a larger, collator unit. Many texture based models posit the use of collator units to detect a boundary or contour (e.g. Wolfson and Landy, 1999). In the fully aligned case (d), the filter covering the gap would signal a discontinuity. However, there could be less noise added into its output into the collator unit. Although on either side of the gap, the stimulus is the same and can be aligned, the gap in itself is an indication of a discontinuity. These results are consistent with findings from Westheimer and Ley (1997) and Brincat and Westheimer (2000). In both studies, the authors report that orientation thresholds for a single short line can be impaired by the presence of a parallel flanker with an orientation difference as small as 1 arcmin. They attribute this to a very narrow bandwidth of orientation summation between lateral receptive fields. In our experiments, when the center and surround are composed of different spatial structures (Fig. 13b) performance is the same as in the single patch condition. This implies that outputs from filters on either side of the gap are not pooled together, possibly because signals from neurons with different spatial preferences are not pooled together.

Although simple-cell like filters could signal a discontinuity across the gap, the amount of noise that they would introduce into the orientation signal would be insufficient to degrade performance substantially. A possible mechanism for the aligned and out-of-phase results in Fig. 9 (Experiment 4) may involve the non-homogenous pooling of parts of the image. In a recent paper by Popple and Levi (2000), the authors suggest a possible mechanism whereby segmentation might affect how orientation signals are pooled. Using a phase-induced orientation illusion to measure orientation pooling, the authors report that the visual system integrates orientation signals over a long range of processing (at least 10°). Popple and Levi suggest that a model which pools orientation signals selectively from a particular portion of the image may account for their results. They propose that focal attention or contour formation mechanisms could determine the region over which orientation pooling occurs. In our experiments, a higher level mechanism could determine whether orientation signals should be pooled together between the center and surround (e.g. pooled when similar), and how much of the image should be used for the pooling process. Our results indicate that segmentation cues influence the pooling stage. In addition to the selective

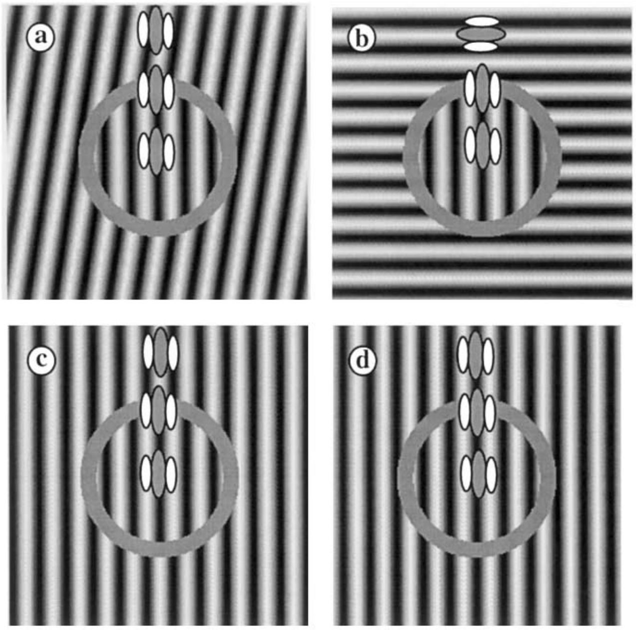

Fig. 13. Explanation of performance in terms of 'good continuity' between information in the center and the surround. Only in d could receptive fields positioned over the two surfaces signal the same object on either side of the gap. In this case, if center and surround are bound, performance approaches that using a full field stimulus. If information from the center and surround signal different objects, performance decreases suggesting interactions between filters located in these two areas. In b, although signals indicate two objects, interaction might be reduced based on physiological reports of little interaction between orthogonally oriented filters.

pooling, we propose that additional noise is introduced in the combination process of the two orientation signals when there is some indication of a mismatch between the two structures from which the orientation signals arose.

To recapitulate, we suggest that there is initial orientation pooling of signals from low-level filters in the center and surround separately, and this provides information about the gap (whether a mismatch is present or not). The outputs of these two orientation pools are combined (if center and surround are sufficiently similar) at a later stage by a higher level mechanism that pools the signals anisotropically. This higher level also introduces additional noise into the overall orientation combination. The finding that a small offset in either orientation or phase between the center and surround leads to increased orientation thresholds suggests that the visual system is very sensitive to small spatial mismatches between different structures. That these mismatches have deleterious effects on orientation discrimination might be a consequence of erroneous binding between neural representations of structures.

Acknowledgements

This research was supported by National Eye Institute grants R01EY 08300 to Michael Hawken and R01EY 01472 to Robert Shapley. We would like to thank Peter Bex, Steven Dakin, Frederick Kingdom and Denis Pelli for helpful comments.

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